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Influence of Cropping on Ca, K, Mg, and Carbohydrate Status of 'French' Prune Trees Grown on Potassium Limited Soils[1]

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Abstract. **'French' prune (*Prunus domestica* L.) leaves on nonbearing trees and large scaffold limbs had greater percent dry matter and specific leaf weight than those from bearing ones early in the season. This difference disappeared as the season progressed. Much of the difference could be attributed to the greater accumulation of starch, which displaced water. The demand for photosynthates by the crop was also reflected by lower starch content in 1-year-old shoot, limb bark, and roots, but no difference in the soluble carbohydrate content nor in the ratio of sorbitol + sucrose/glucose + fructose was observed. Leaf K content was influenced by the crop but not Ca and Mg contents. Unlike K contents, Ca contents in fruiting spurs and 1-year-old shoots tended to be greater than those from nonbearing samples; no differences were noted in root samples. These data and those of other workers indicate that K deficiency in this cultivar stems from its strong K demand by the fruit and from the lack of carbohydrates being translocated to the roots, which in turn, limits growth and nutrient uptake, especially K, which is limiting in these soils.**

'French' prune trees growing on certain soil series in California exhibit chlorosis, leaf scorch, and shoot die-back, which are typical K deficiency symptoms when the trees bear a moderate to heavy crop. Leaf K content decreased as the crop matured in orchards located in these areas (14). Lilleland (unpublished) has shown that this K depletion can be arrested by foliar sprays of KNO_3 but not readily by soil applications. Questions arise as to what mechanisms are involved by which the maturing fruit govern nutrition of the tree. Is it a localized phenomenon, where K is exported from leaves to the fruit along with photosynthates as in the case of pecans (22) and pistachios (25), or does the influence extend beyond adjacent limbs and as far as the roots? Barden (1) found that net photosynthesis and specific leaf weight correlated with light intensity. Similar evidence was found in bearing walnuts (20). However, in other species where the source-sink gradient was relatively steep, photosynthetic efficiency was seemingly increased (2, 7, 9, 12, 17). To assess this effect of fruiting on the distribution of carbohydrates and mineral elements, K, Ca, and Mg in 'French' prune trees, differentially thinned trees in 3 orchards having previous histories of severe potassium deficiency were studied.

Materials and Methods

Three orchards of 'French' prunes, (syn. 'petite d'Agen') were selected in the Sacramento Valley where K deficiency symptoms, i.e., leaf scorch and limb die-back, occur in years of heavy crops. Hereafter, the orchards will be referred to as sites A, B, and C. On May 5, six uniform trees bearing moderate crops were chosen, of which 2 were completely defruited, and 2 had alternate scaffold branches defruited, while the remaining pair was kept intact as the bearing control. Periodically, leaves, fruits, and shoots from these trees and from those adjacent to the test trees manifesting various degrees of leaf scorch were analyzed for K, Ca, and Mg. A root sample was gathered at side C at harvest.

Sampling and sample preparation. At 2- to 3-week intervals, 100 spur leaves were collected from each tree and brought to the laboratory in a cold box. Fifty fruits were collected for determining their size and composition. On June 2, July 25, and August 15, five shoots each from the current season's growth and that of the previous year were collected. On June 2 and August 15, ten bark discs were obtained from each tree with an 18-mm diameter cork borer. Roots larger than 4 mm diameter collected at site C were subdivided into wood and bark tissues, while those which were smaller were not. Samples were lyophilized after their fresh weights were determined.

Specific leaf weight (SLW). Leaf discs from 70 to 90 leaves were obtained with a 18-mm diameter cork borer. SLW (cg dry matter dm^{-2}) was derived by dividing the dry weight by the area of the discs.

Sugars and sorbitol. A 4-ml aliquot from a 100-ml ethanolic extract, representing 2.0 g of freeze-dried sample was evaporated to dryness after adding 1.0 mg of trehalose as an internal standard. The dry residue was then silyated according to Sweeley et al. (24). The amount of soluble carbohydrates in the samples was determined by gas chromatography (Varian Aerograph, Model 1400, fitted with a stainless steel column, 120 mm × 0.3 cm, filled with 3.8% SE 30 coated on Chromsorb W, 100/200 mesh).

Starch analysis. The alcohol-insoluble substances (AIS) remaining after sugar extraction were preboiled to hydrate the starch grains and then subjected to 24-hr incubation with purified diastase in acetate buffer, pH 5.0. Upon filtering the mixture, the sugar in the hydrolysate was determined colorimetrically using anthrone (23).

Mineral analyses. A 500-mg subsample of dry matter was digested with HNO_3 on a sand bath at 130°C, after which any organic residue remaining was oxidized with a few drops of

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H_2O_2. On adjusting the volume, K was determined by flame emission spectroscopy while Ca and Mg were determined by atomic absorption spectroscopy (Varian Techtron, Model 120) (21).

Results and Discussion

Dry matter assimilation by leaves. Fresh and dry leaf weight from bearing and nonbearing limb units and trees varied from one sampling date to the next. However, the mean weight of those from nonbearing units was consistently greater than the mean weight from bearing ones (data not shown). The percent dry matter of leaves from nonbearing trees was, likewise, consistently greater than that from nonbearing limbs or bearing units until September, when they became equal (Fig. 1a). Moisture content on leaf area basis (cg H_2O/dm^2)was the same among samples until late summer, when those gathered from nonbearing trees remained higher than the others (Fig. 1b). SLW (cg dry matter dm^{-2}) of samples from nonbearing trees was consistently greater than that from bearing ones in 29 out of 33 samples; 3 were of equal value while the initial value at site C was lowest. The seasonal trends of the means are shown in Fig. 1c. Dry matter accumulation expressed as percentage of SLW increased with age, but that from bearing units ceased to increase during July and decreased slightly in early August, only to increase after fruit harvest was completed. This temporary cessation of dry matter accumulation by leaves is attributed to the demand for photosynthates created by the fruit which increased 2.5 g during the same period (Fig. 2). This phenomenon of accelerated export of photosynthates as a function of fruit growth rate in prunes was demonstrated by Hansen and Ryugo (9) utilizing $^{14}CO_2$. Less leaf starch and smaller SLW may be additional evidence of this phenomenon. Under similar circumstances where the source-sink gradient was steepened by the maturing fruit, net photosynthesis was increased in peaches (19), apples (6, 8, 10), and grapes (2). The presence of tubers on potato plants and roots on bean leaf petioles (11) also increased net assimilation rates for the same reason.

Whereas the SLW on nonbearing trees decreased, and whereas it became constant on comparable limb units after August 23, it tended to increase on previously bearing units (Fig. 1c). The decrease of SLW in nonbearing trees may be an indication of early senescence and remobilization of nutrients to the spurs. Early senescence in 'French' prunes is a common observation in nonbearing or light-cropping trees. If, for some reason, flowers or fruits do not set, leaves will often turn yellow in late August and prematurely abscise. This may account for the lower starch content in leaves of nonbearing units than that from bearing ones in the September 9 samples from site C (Table 1). The

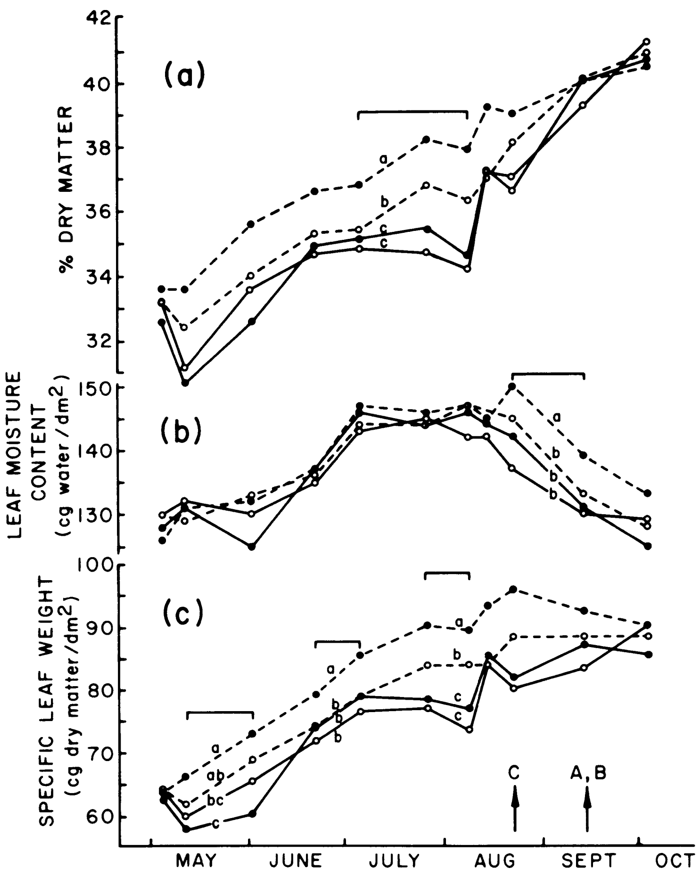

Fig. 1. Seasonal changes in percent dry matter (a), moisture content per unit leaf area (b), and specific leaf weight (c) of 'French' prune leaves sampled in 3 orchards known to have limited soil potassium. The curves represent samples taken from bearing (———) and nonbearing (-----) trees (solid dots) and limb units (open circles). Significant differences at 95% confidence level is noted by different letters between dates covered by the horizontal bars. The vertical arrows indicate the dates of harvest at sites A, B, and C.

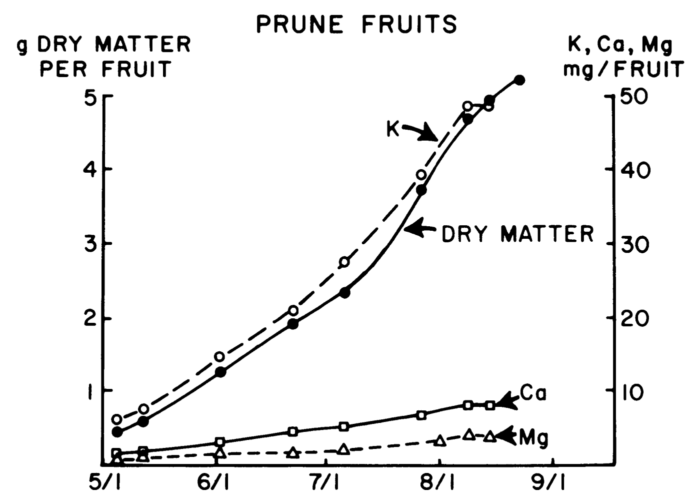

Fig. 2. Seasonal accumulation of dry matter, K, Ca, and Mg per 'French' prune fruit at site C.

Table 1. Seasonal changes in 'French' prune leaf starch content[z] by orchard sites and treatments.

Sampling & harvest dates	Site	Leaf starch content (% dry wt)			
		Trees		Limbs	
		+ fruit	− fruit	+ fruit	− fruit
May 5	A B C	4.3	10.0	5.4	8.2
July 27 & Aug. 9[y]	A B C	1.8	5.3	1.7	2.8
Aug. 23	A B --	0.8	2.1	0.7	1.6
Aug. 23[x]	-- -- C	6.9	5.5	7.2	4.0
Sept. 9[x]	A B --	3.5	3.0	2.8	2.8
Sept. 9	-- -- C	10.8	6.0	9.9	7.8

[z]Least significant difference at 5% level is 1.1.
[y]Samples were combined for these dates.
[x]Crops harvested on this date; mature fruit dropping.

increasing amount of starch displacing water could account for most of the concurrent decrease in moisture content (Fig. 1b).

Carbohydrate levels in 1-year-old shoot, bark of scaffold limbs, and roots. Starch content in 1-year-old bearing and nonbearing shoots on June 2 showed a slight difference, the latter storing as much or more reserve food than the former (Table 2). This difference diminished as the fruits approached full size towards harvest. Bark samples taken from nonbearing trees contained more starch than those from bearing trees, which confirms our earlier finding with this species (21). Similar results reflecting sink strength of the crop were shown in 'Sugar' prune (2), apples (17), and walnuts (20). Comparison between limb units revealed no significant difference (Table 2). Analysis of 14 samples of wood and bark from large roots and intact small roots manifested no significant difference within treatment, but between treatments, those from nonbearing trees contained about 3 times more reserve food than those from bearing ones (Table 2). Analyses of limbs for soluble carbohydrates revealed that fruit removal had little or no effect on their concentrations (data not shown). The ratio of sucrose and sorbitol, the principal translocated carbohydrates, to glucose and fructose did not change. It appears that in the absence of a crop, these mobile carbohydrates are metabolized to starch in the stem storage cells, and the surplus is routed to other sinks.

Fruit development. Fruits on partially defruited trees consistently contained more dry matter per fruit than those from unthinned control trees (Table 3). This response—increased fruit size by the crop on a large scaffold limb because of fruit removal from an adjacent one—is seldom observed. While some photosynthates may be translocated from one limb to another, fruit size increase observed here is attributed to the lessening of the gradient between the leaves and fruits on the bearing units; the nonbearing units presumably supplied much of the needs for the remainder of the tree. Davis (4) found little evidence of flower-inducing substances being translocated from a nonbearing 'Sugar' prune scaffold limb to an adjacent bearing one. That the direction and rate of photosynthate flow depended on the size and proximity of the sinks was also observed in apples (6).

K and Ca accumulation. Initial leaf K content on dry weight basis varied from tree to tree within the same site (not shown) and subsequently fluctuated among the 3 sites according to treatment. Therefore, no definite trend was discernible. However, when the data were computed on a relative scale based on the initial concentration (Fig. 3), or on the increase or decrease over the initial value based on leaf area, some of the variations disappeared and trends became apparent (Fig. 4). Since fruit removal was done on May 5 after the leaves had attained maximum size, the values presented on area basis probably approximate the changes in concentration on a per cell basis better than on a dry weight basis. On a leaf-area basis, K content in leaves from defruited limbs at site B remained consistently low, while at sites A and C, the values exceeded those of bearing trees or limbs only between July 27 and September 9. There is no explanation why K levels in bearing trees and limbs increased and then decreased at site A, while comparable units remained nearly constant at site B; and only that of bearing trees increased steadily at site C. The decrease in K level on nonbearing trees at sites A and B may be another reflection of early senescence of leaves. K well could have been exported with carbohydrates and nitrogenous constituents during the remobilization of nutrients by the spurs.

Table 2. Comparison in starch content between parts of bearing and nonbearing 'French' prune trees and limb units[z] sampled at different times during the growing season.

		Starch content (% dry wt)			
		Trees		Limbs	
Tree part	Sampling date	+ fruit	− fruit	+ fruit	− fruit
1-year-old shoots	June 2	2.9a[x]	4.5b	—	—
1-year-old shoots	July 27	6.9a	8.0a	6.9a	6.9a
1-year-old shoots[z]	Aug. 15	7.5a	8.2a	7.3a	8.7a
Bark, scaffold	June 2	1.2	3.6	—	—
Bark, scaffold	Aug. 15	3.0a	6.8c	4.0ab	5.6bc
Roots[z, y]	Aug. 23	4.4a	12.6b	—	—

[z]Values represent site C, otherwise, they are averages of all sites.
[y]Represent mean values of 14 small and large root samples which were not significantly different within treatment.
[x]Different letter within treatments on the same sampling date indicate significant differences at 5% levels of confidence.

Table 3. Comparison of dry matter accumulation by fruit between unthinned and partially thinned[z] 'French' prune trees at sites A and B.

	Dry matter accumulation (g/fruit)					
Treatment	June 22	July 6	July 27	Aug. 9	Aug. 15	Aug. 23
Unthinned trees	1.19	1.53	2.88	3.84	3.86	4.52
Thinned trees[z]	1.31	1.68	3.18	4.09	4.52	5.12

[z]Alternate scaffold limbs completely defruited on May 5. No significant difference in fruit size between differentially treated trees at each site at onset of experiment.

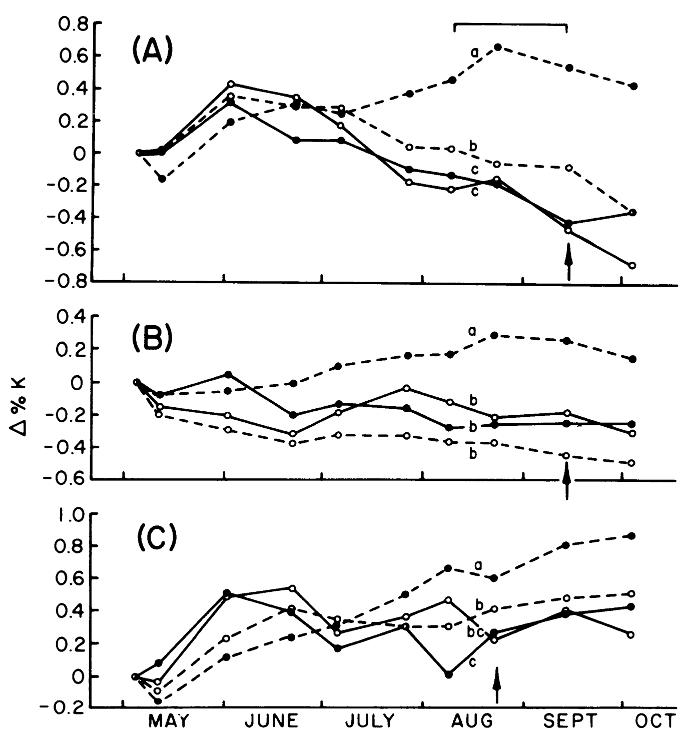

Fig. 3. Seasonal changes in percent K of 'French' prune leaves based on initial value on May 5 when nonbearing trees and limbs were defruited at sites A, B, and C. The symbols are the same as those in Fig. 1.

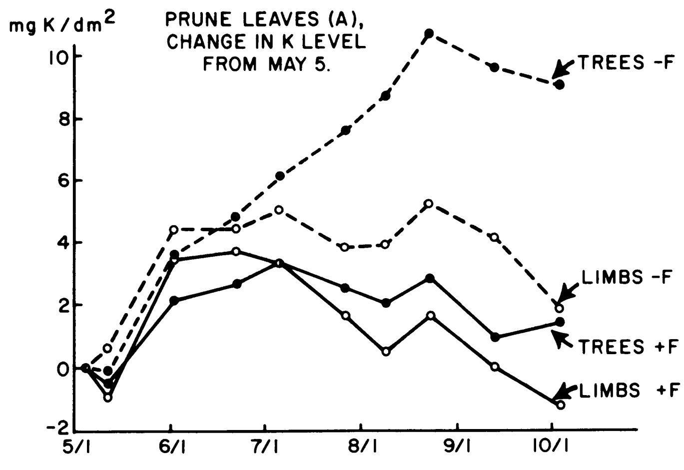

Fig. 4. Seasonal changes in K content on leaf area basis (mg K/dm^2) expressed as more or less than the initial sample taken on May 5. Trees at site (A) have previous histories of manifesting potassium deficiency symptoms in years of heavy crops. The symbols +F and −F indicate bearing and nonbearing units, respectively.

Analyses of leaves gathered from trees disclosing no symptom of leaf scorch and those exhibiting varying degrees of this disorder revealed that K content decreased proportionally with the severity of this symptom, while Ca and Mg contents were unchanged (Table 4). Since the scorch symptom appears over the entire upper surface of the foliar canopy, it indicates that the xylem stream is depleted of K during its upward movement and/or the element is remobilized from the extremities to satisfy the demand of the growing fruit.

Table 4. K, Ca, and Mg content in leaves sampled from normal symptomless 'French' prune trees and adjacent ones manifesting varying degrees of leaf scorch.

		Element content (% dry wt)			
		Normal trees	K-deficient trees		
Element	Sampling date	Scorch rating None	None	Scorch rating Moderate	Severe
K	Aug. 9	1.64	0.43	0.20	0.14
	Aug. 23	1.88	0.41	—	—
	Oct.4	2.06	0.54	—	—
Ca	Aug. 9	2.66	2.67	2.75	2.54
Mg	Aug. 9	0.72	1.04	1.19	1.16

Dry matter accumulation by the fruit accelerated slightly after July 5 (Fig. 2) while mineral uptake seemingly kept pace. Fruit K content changed insignificantly between July 5 and August 15 from 1.2 to 1.0%, while Ca and Mg contents remained about constant during the same period at 0.18 and 0.08%, respectively. Hence, there was no dilution effect with the increase in fruit size. In pecans, the accumulation of K by the shuck of the nut was accompanied by a simultaneous reduction in leaf K content (22). In the pistachio, the leaf K was higher in bearing shoots than leaf K in nonbearing ones on the same trees (25). It should be pointed out that the bearing pistachio shoots will elongate more than the nonbearing ones on the same tree, even though the leaves on the former may exhibit temporary chlorosis when the crop begins to accumulate dry matter in mid-summer.

Ca content as percent dry matter is consistently lower in leaves gathered from nonbearing units than that from bearing ones (data not shown). But the percent dry matter and SLW of nonbearing leaves are consistently greater than those of bearing ones; thus, this difference in Ca content may merely reflect growth dilution.

Analyses of current growth, 1-year-old shoot, scaffold bark, and roots revealed that nonbearing samples were always richer or equal to the comparable bearing ones with respect to K (Table 5), but the situation was reversed with respect to Ca. Young shoots collected from trees exhibiting scorch symptom were lower in K content but this difference was not clear cut in bark or fruit samples (Table 6). These results confirm earlier contentions that Ca and Mg are not as mobile as K (7), and therefore, their levels in leaves are relatively unaffected by the presence or absence of the crop.

During the bearing cycle, starch content in roots of 'Sugar' prunes was less than half of the nonbearing ones by May (4). Our analyses showed that even a moderate crop limited export of photosynthates and accumulation of reserve food in roots. Head (10) demonstrated that defoliation or heavy fruiting in apple trees altered the trends of new root formation. Kazaryan and Arutyunyan (12) found that cropping influenced carbohydrate and nitrogen metabolism of apple tree roots. This evidence lead us to believe that heavy cropping greatly limited root growth and activity of prune trees. A decrease in absorbing surface prevents thorough exploration of the soil mass while lack of carbohydrates limits nutrient and water uptake. Thus, in areas where soil K is limiting, heavy cropping leads to depletion of foliar K while reducing K uptake by roots.

Table 5. K and Ca content in different parts of 'French' prune trees.

			Element content (% dry wt)			
			Trees		Limbs	
Element	Sampling date	Part of tree	+ fruit	− fruit	+ fruit	− fruit
K	Aug. 15	Current growth	0.19a[z]	0.34c	0.19a	0.24b
	Aug. 15	1-yr-old shoot	0.15a	0.28c	0.17ab	0.20b
	Aug. 15	Limb bark	0.19a	0.30b	0.18a	0.19a
	Aug. 23	Roots	0.20a	0.25a	—	—
Ca	Aug. 15	Current growth	1.29a	0.87b	1.17a	0.87b
	Aug. 15	1-yr-old shoot	1.14c	0.93a	1.20c	1.01ab
	Aug. 15	Limb Bark	2.12a	1.80a	2.12a	1.88a
	Aug. 23	Roots	0.16a	0.15a	—	—

[z]Letters denote LSD at 5% level between treatments. The percentages on dry weight basis are means of 3 orchards.

Table 6. Potassium content in shoots and fruits of 'French' prune trees exhibiting different severities of leaf scorch. Samples taken on August 15.

Sample parts	K content (% dry wt)			
	Scorch rating			
	None	Slight	Moderate	Severe
Current growth	0.17	0.18	0.08	0.07
1-year-old shoot	0.14	0.15	0.13	0.08
Bark of limbs	0.30	0.13	0.10	0.15
Fruit	1.17	0.95	0.91	0.90

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